A TAXONOMIC REVIEW OF THE LANTERNFISH GENUS *TRIPHOTURUS* FRASER-BRUNNER, 1949 (MYCTOPHIDAE, OSTEICHTHYES)

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(With 8 figures and 3 tables)

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ABSTRACT

The genus *Triphoturus* includes two known species: *Triphoturus nigrescens* (Brauer, 1904) and *Triphoturus mexicanus* (Gilbert, 1890). For the latter species, a southern population and a northern population may be distinguished on the basis of gill-raker counts. Phenotypic variation in serial meristic data may be environmentally induced in the northern population, accounting for differences between specimens from the California Current region and from the Gulf of California. The two species are described, together with comments on their distributions, including the first records of *Triphoturus nigrescens* in the Atlantic Ocean; here this species possesses an Agulhas Subpattern of distribution. A lectotype (ZMB 17617) is designated for *Myctophum (Lampanyctus) nigrescens* Brauer, 1904.

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INTRODUCTION

The subgenus *Triphoturus* was created by Fraser-Brunner (1949) to include five species: *Lampanyctus microchir* Gilbert, 1913; *Myctophum (Lampanyctus) micropterum* Brauer, 1906 (with *Myctophum oculeum* Garman, 1899, being considered a junior synonym); *Myctophum (Lampanyctus) nigrescens* Brauer, 1904; *Serpa turneri* Fowler, 1934; and *Myctophum mexicanum* Gilbert, 1890. On the basis of osteological and photophore evidence, Paxton (1972) raised the status to that of a genus, phylogenetically closely related to *Lampanyctus* Bonaparte, 1840, but distinguished from it by the possession of five VO photophores and by the presence of a small dorsal process on the opercular head of the hyomandibular. Later, in his list of nominal genera and species, Paxton (1979) included two definite species, *Myctophum mexicanum* Gilbert (with the questionable junior synonym *Myctophum oculeum*) and *Myctophum (Lampanyctus) nigrescens* (with the questionable junior synonym *Lampanyctus microchir*), and one possible species (*Myctophum (Lampanyctus) micropterum*), within the genus *Triphoturus*.

However, the taxonomic status of the species of the genus is still unresolved (Hulley 1984). The type-series of *Myctophum (Lampanyctus) micropterum* Brauer, 1904, comprises two species (Hulley 1981): *Lampanyctus isaacsi* Wisner, 1974 (ZMB 17614, 17615—Gulf of Guinea) and *Triphoturus micropterus* (Brauer, 1906) (ZMB 17616—east of Seychelles), with the latter specimen designated as the lectotype for the purposes of stability. Further, no differences between this lectotype and the descriptions of *Triphoturus microchir* (Gilbert) given by Gilbert (1913) and Nafpaktitis & Nafpaktitis (1969) were observed, so that *Triphoturus microchir* was synonymized with *Triphoturus micropterus* (Hulley 1981). On the other hand, Wisner (1976) synonymized *Triphoturus microchir* (Gilbert) with *Triphoturus nigrescens* (Brauer, 1904), as there appeared to be no differences warranting the retention of Gilbert's species.

Brewer (1973) and Wisner (1976) suggested, not only on the basis of numbers of vertebrae and gill rakers but also on the distinctiveness of the larvae (Moser & Ahlstrom 1970; Ahlstrom 1971), that *Triphoturus mexicanus* is a species-complex consisting of two species: a 'southern' species referable to *Triphoturus oculeus* (Garman), and a 'northern' species referable to *Triphoturus mexicanus* (Gilbert). Further, Wisner (1976) stated that the latter species consists of two probable, but as yet unnamed, subspecies—one occurring in the Gulf of California from 30°N to 18°N, and the other in oceanic waters of the California Current between 38°N and 20°N, with a southern extension to 13°N in the region of 127°W. A similar distinction was drawn by Robison (1972) on the basis of higher relative abundance values in the Gulf of California. For the *Triphoturus mexicanus*-complex Imsand (1982, figs 22, 23, 25) differentiated: (1) a Gulf of California population from a California Current population (both termed *Triphoturus mexicanus*) on the criterion of occurring in areas south and east of 23°N 111°W; and (2) a southern population (termed *Triphoturus oculeus*) from the two northern populations, on the criterion of occurring south of 16°N. She stated, however, that these populations are allopatric, with very few areas where individuals of the two populations can be captured in the same net tow (Imsand 1982, fig. 26).

The purpose of the present paper is to clarify the species composition of the genus *Triphoturus* by the examination of the types and other material.

METHODS

The material examined is listed separately under each species in the Systematic Account. The species are listed alphabetically and type localities are given in parentheses in the synonymies. Methods for taking measurements and counts follow Nafpaktitis (1973). A total of 13 morphometric measurements, each to the nearest 0,1 mm, were made on each specimen with needle-point callipers and using a binocular dissecting microscope where necessary. These include: SL—standard length; HL—head length; HD—head depth; BD—body depth; UJ—upper jaw length; ED—eye diameter; CPL—caudal peduncle length; CPD—caudal peduncle depth; PreD—predorsal length; PreAd—preadipose length; PreP—prepectoral length; PreV—preventral length; PreA—preanal length. A total of six meristic counts were made on each specimen, including: D—dorsal rays; A—anal rays; AOa—AOa photophores (left and right); AOp—AOp photophores (left and right); [AOt = AOa + AOp]; GRu—gill rakers on upper limb (left); GRl—gill rakers on lower limb (left); [GRt = GRu + 1 + GRl].

Photophore groupings are in accordance with Paxton (1972) and their abbreviations are given by Hulley (1981). The following additional abbreviations are used in reference to material examined:

CAS — California Academy of Sciences, San Francisco, USA
LACM — Los Angeles County Museum of Natural History, Los Angeles, USA
MCZ — Museum of Comparative Zoology, Harvard, USA
SAM — South African Museum, Cape Town, RSA
SU — Stanford University Natural History Museum, Stanford, USA (specimens now housed in CAS)
USNM — National Museum of Natural History, Washington DC, USA
ZMB — Zoologisches Museum, Berlin, GDR

Statistical analyses and scatter plots were performed on an Apple IIe computer using STATPRO (Wadsworth Electronic Publishing Company) and standard reference texts (Snedecor & Cochran 1967; Sokal & Rohlf 1969; Zar 1974). Computer programmes for analysing morphometric data to allow for size-free comparisons of shape among specimens (Humphries *et al.* 1981; Johnson & Feltes 1984) were not available to the author. Meristic data were plotted according to the method of Hubbs & Hubbs (1953).

RESULTS

Where possible, morphometric data (in mm) and meristic data for the type specimens are given in Table 1. These specimens and the additional material have been divided into five groups for the purposes of analysis, with the number of specimens given in parentheses:

Group A. California Current region: meristics—CAS 24312 (30), LACM 39201-1 (48), SAM-24926 (3); morphometrics—CAS 24312 (30).

Group B. Gulf of California: meristics and morphometrics—SU 68 (2), SU 46808 (30).

Group C. Middle American Trench: meristics—LACM 31125-27 (27).

Group D. Central and eastern South Pacific: meristics—LACM 33603-18 (3), LACM 33676-7 (4), LACM 33696-11 (4), MCZ 28500 (3), MCZ 35185 (1),

TABLE 1

Triphoturus. Measurements (in mm) and counts of examined type specimens.

Species	Status	No. of speci-mens	Catalogue No.	SL	HL CPD D	HD PreD A	BD PreAd AOa	UJ PreP AOp	ED PreV GRu	CPL PreA GRl
M. mexicanum	lectotype	1	USNM 76343	42,8	—	—	—	—	—	8,6
					—	21,6	—	—	—	—
					12	14	4	6	4	10
	paralectotypes	2	SU 68	52,5	16,1	8,8	9,6	10,4	3,7	12,1
					4,1	25,4	39,9	15,7	22,0	30,0
					13	15	—	—	4	13
				50,4	15,3	8,6	9,0	10,7	4,0	10,9
					4,1	24,4	38,6	16,1	22,8	30,3
					13	16	4	6	4	12
M. oculeum	syntypes	3	MCZ 28500	58,4	16,8	9,1	10,4	11,8	5,0	—
					4,9	28,2	45,6	—	—	34,4
					13	—	—	—	3	10
				28,6	8,9	5,2	5,4	6,4	1,9	5,7
					2,0	15,1	22,2	9,4	13,2	16,9
					—	15	—	—	3	10
				(37)#	—	—	—	—	—	—
					—	—	—	—	—	—
					—	—	6	—	3	10
	syntype	1	MCZ 35185	54,9	15,4	8,5	9,0	11,4	4,1	—
					4,2	27,8	44,1	16,7	23,7	33,7
					13	15	5	—	3	11
	syntype	1	MCZ 35187	44,0	13,0	7,4	7,9	8,3	2,9	9,0
					3,6	21,8	34,7	12,7	18,6	26,8
					12	16	5	5	4	10
L. microchir	holotype	1	USNM 74468	17,0	5,1	3,2	3,1	4,0	0,8	4,0
					1,1	9,3	13,4	5,6	—	9,4
					(14)	(17)	4	6	3	8
M. micropterum	syntype†	1	ZMB 17614	74,7	18,1	11,0	11,3	14,5	3,8	16,1
					6,3	33,9	55,0	21,1	28,5	38,9
					15	17	6	7	5	13
	syntype†	1	ZMB 17615	21,0	—	—	—	—	—	—
					—	—	—	—	—	—
					—	—	6	7	5	12
	syntype*	1	ZMB 17616	18,2	—	—	—	—	—	—
					—	—	—	—	—	—
					15	16	5	6	3	8
M. nigrescens	syntype	1	ZMB 17617	29,3	—	5,0	5,0	6,1	1,9	—
					1,8	16,6	23,1	9,2	13,6	17,4
					14	—	4	6	3	8
	syntype#	1	ZMB 22379	(10)	—	—	—	—	—	—
					—	—	—	—	—	—
					—	—	—	—	—	—

†—*Lampanyctus isaacsi* Wisner, 1974 (*fide* Hulley 1981)
*—lectotype of *M. micropterum*—*fide* Hulley (1981)
#—specimen dried out or damaged

TABLE 2

Triphoturus. Morphometrics: standard length (SL) in millimetres; all other distances expressed as percentages of SL.

	n	SL	HL	HD	BD	UJ	ED	CPL	CPD	PreD	PreAd	PreP	PreV	PreA
Group A	30	39,5–62,0	28–35	14–18	15–19	19–23	6–8	20–24	7–10	47–53	74–88	28–36	40–47	56–66
Group B	30	22,7–59,7	30–33	17–19	18–20	20–23	6–9	19–22	8–10	47–51	74–81	30–34	40–46	57–63
Group D	11	28,6–69,0	25–32	14–18	16–19	17–22	6–8	19–23	7–9	46–53	75–81	26–33	39–46	57–63
Group E	20	13,1–33,4	27–31	13–17	12–17	18–23	5–7	19–25	5–7	50–55	76–81	28–33	42–45	55–61

MCZ 35187 (1), MCZ 56962 (5); morphometrics—LACM 33603–18 (2), LACM 33696–11 (2), MCZ 28500 (2), MCZ 35185 (1), MCZ 35187 (1), MCZ 56962 (5).

Group E. South African region: meristics (22) and morphometrics (26); for details see Table 3.

Morphometric data (expressed as the range of the measurement as a percentage of SL) for these groups are given in Table 2. Scatter plots of relevant morphometrics are given in Figures 1–3, and meristic data are presented in Figure 4.

TABLE 3

Triphoturus nigrescens. Collection data on SAM specimens.

SAM Cat. no.	Station no.	Date	Position		Depth (m)	Gear	No.	Size (mm)	Remarks
27309	IK 6	23.04.1961	west of Cape Town		200–0	IKMT	1*	—	meristics only
27310	A 2967	28.03.1964	37°45′S	18°00′E	600–0	IKMT	1	32,7	
27311	A 1896	11.07.1962	34°12′S	28°24′E	1000–0	N200B	1	33,4	
27312	A 2961	22.03.1964	40°12′S	14°41′E	700–0	IKMT	1	25,4	
28091	SM 125	10.05.1977	30°32,2′S	30°57,5′E	415–0	RMT	1	28,2	
28092	SM 153	17.05.1977	30°15,5′S	31°28,2′E	664–0	RMT	1	31,8	
28093	SM 148	17.05.1977	30°17,1′S	31°25,2′E	750–0	RMT	3*	—	meristics only
28094	SM 157	18.05.1977	30°05,5′S	31°57,0′E	750–0	RMT	1	33,0	
28308	SM 190	01.06.1978	34°06,3′S	27°08,3′E	658–0	RMT	3	23,3–27,9	
28324	SM 173	28.05.1978	33°25,2′S	27°54,7′E	683–0	RMT	1	30,8	
28346	SM 167	27.05.1978	33°10,5′S	28°17,5′E	1091–0	RMT	1	24,95	
29040	SM 104D	24.05.1976	28°25,6′S	32°44,5′E	200–0	Bongo	1	17,0	
29062	SM 70D	20.05.1976	27°23,9′S	33°02,9′E	200–0	Bongo	1	16,2	
29070	SM 143D	15.05.1977	31°14,7′S	30°14,7′E	212–0	Bongo	2	17,9–28,6	
29146	SM 80	21.05.1976	27°39,0′S	33°00,0′E	359–0	Bongo	1	13,1	
29365	SM 62S	19.05.1976	27°10,2′S	33°10,3′E	45–0	Bongo	1	26,1	
29791	2013	09.08.1982	33°40,0′S	14°41,8′E	50	RMT-2	2	20,3–29,2	
29956	2023	10.08.1982	33°36,08′S	15°45,25′E	75	RMT-2	1	21,6	
29979	2028	11.08.1982	33°40′S	16°45′E	75	RMT-2	1	26,9	
30016	2070	16.08.1982	29°27′S	14°14′E	25	RMT-2	1	19,8	

*—damaged

DISCUSSION

As pointed out by Johnson & Feltes (1984), the interpretation of serial meristic data is difficult, since variation can be the result of ecophenotypic effects (Barlow 1961; Fowler 1970; Johnson & Barnett 1975). Myctophid taxonomy, however, is based on the nature and orientation of various established photophore groupings. These are, in the main, species-specific, although there may be some minor variation in individual photophore position, e.g. the position of SAO_1 in relation to VO_2–VO_3 in *Lampanyctus ater*. In a few cases (*Protomyctophum normani*-complex and *Symbolophorus boops*-complex) photophore grouping and position may be identical, so that the structure of the secondary sexual characters (the supra- and infracaudal glands) has been employed in distinguishing the species, particularly in the subfamily Myctophinae (Hulley 1981). However, in the tribe Lampanyctini (subfamily Lampanyctinae), the lengths of the supra- and infracaudal glands, rather than differences in structural form, are of diagnostic value, e.g. *Ceratoscopelus* spp., *Lampadena* spp., *Lampanyctus* spp., *Taaningichthys* spp. Variations in the total number of gill rakers on the first arch and variation in the counts of serial meristic characters (fin rays, AO photophores) are of lesser importance, although some exceptions do occur, e.g. in the genera *Notoscopelus* and *Gymnoscopelus*. The number of gill rakers on the lower limb of the first arch may exhibit clinal variation, e.g. *Hygophum taaningi*, while variation in the number on the upper limb of the first arch may be indicative of population structure (*Diaphus dumerilii*, *Hygophum hygomii*, *Lampanyctus alatus*) or may be species-specific, when supported by differences in photophore grouping and/or caudal gland structure (Hulley 1981).

In the *Triphoturus nigrescens* species-group, comprising specimens from the South African region (Group E) and the types of *Lampanyctus microchir*, *Myctophum micropterum* and *M. nigrescens* (Figs 6–7), the VLO is on or before the vertical through the ventral base; PVO_1 is positioned slightly in front of, on, or behind the vertical through PVO_2; and only the VO_2 is elevated and anteriorly displaced to before VO_1. While VO_3 may be slightly raised in some specimens, it is well below the line passing through VO_2 and SAO_1. Further, PO_3 is level with PO_2 and PO_5 and Pol_2 is well in front of the adipose origin. Some variation in individual photophore position does occur, namely PO_4; PVO_1; PVO_2; PLO; SAO_1 (see Description), but this variation is of no taxonomic significance, being encountered even amongst specimens from the same haul. In all specimens of this species-group, the length of the infracaudal gland is less than one-half the length of the caudal peduncle.

In the *T. mexicanus* species-group, comprising specimens from Groups A, B, C, and D, and including the types of *Myctophum mexicanum* and *M. oculeum* (Fig. 5), the VLO is well behind the vertical through the pelvic base; PVO_1 is well before the vertical through PVO_2; and both VO_2 and VO_3 are highly elevated, with VO_3 touching the line passing through VO_2 and SAO_1—the VO_2 is more anteriorly displaced (on vertical through outer ventral base) in the *T. mexicanus* species-group than it is in the *T. nigrescens* species-group (behind vertical

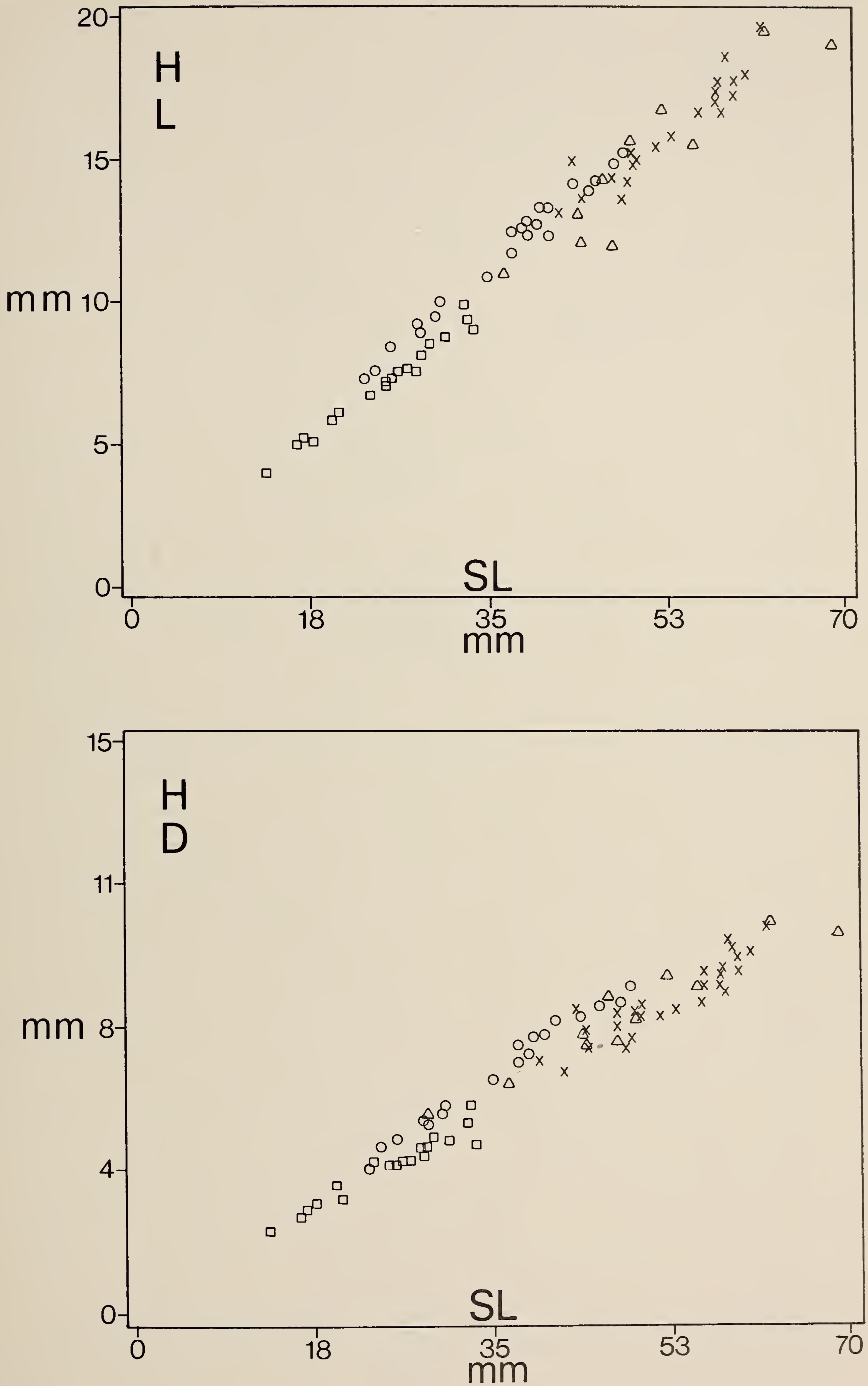


Fig. 1. *Triphoturus.* Upper: head length (HL) plotted against standard length (SL). Lower: head depth (HD) plotted against standard length (SL). Symbols: specimens from Group A, California Current region—cross; Group B, Gulf of California region—circle; Group D, Central and eastern South Pacific region—triangle; Group E, South African region—square. All measurements in mm.

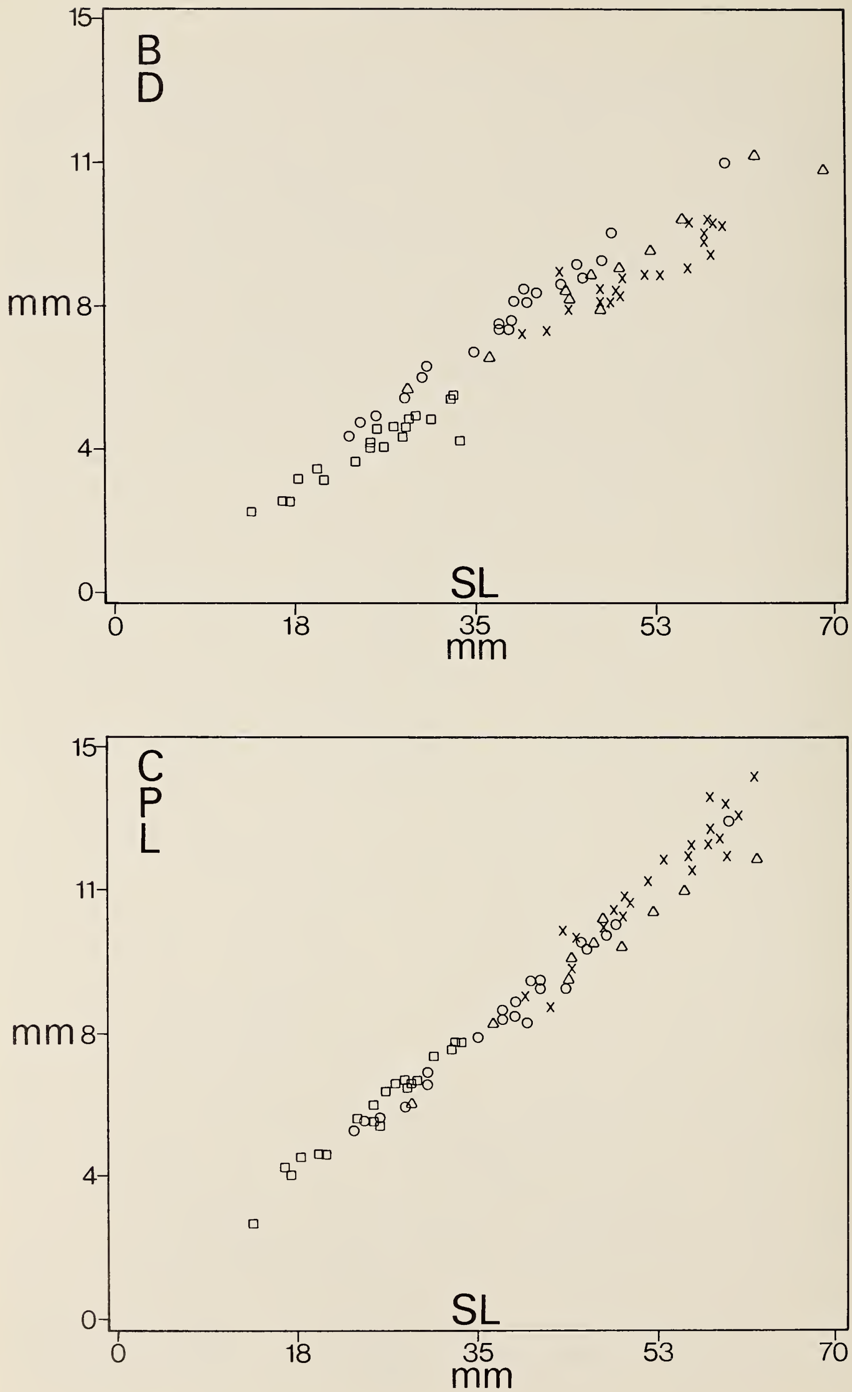


Fig. 2. *Triphoturus*. Upper: body depth (BD) plotted against standard length (SL). Lower: caudal peduncle length (CPL) plotted against standard length (SL). Symbols as in Figure 1. All measurements in mm.

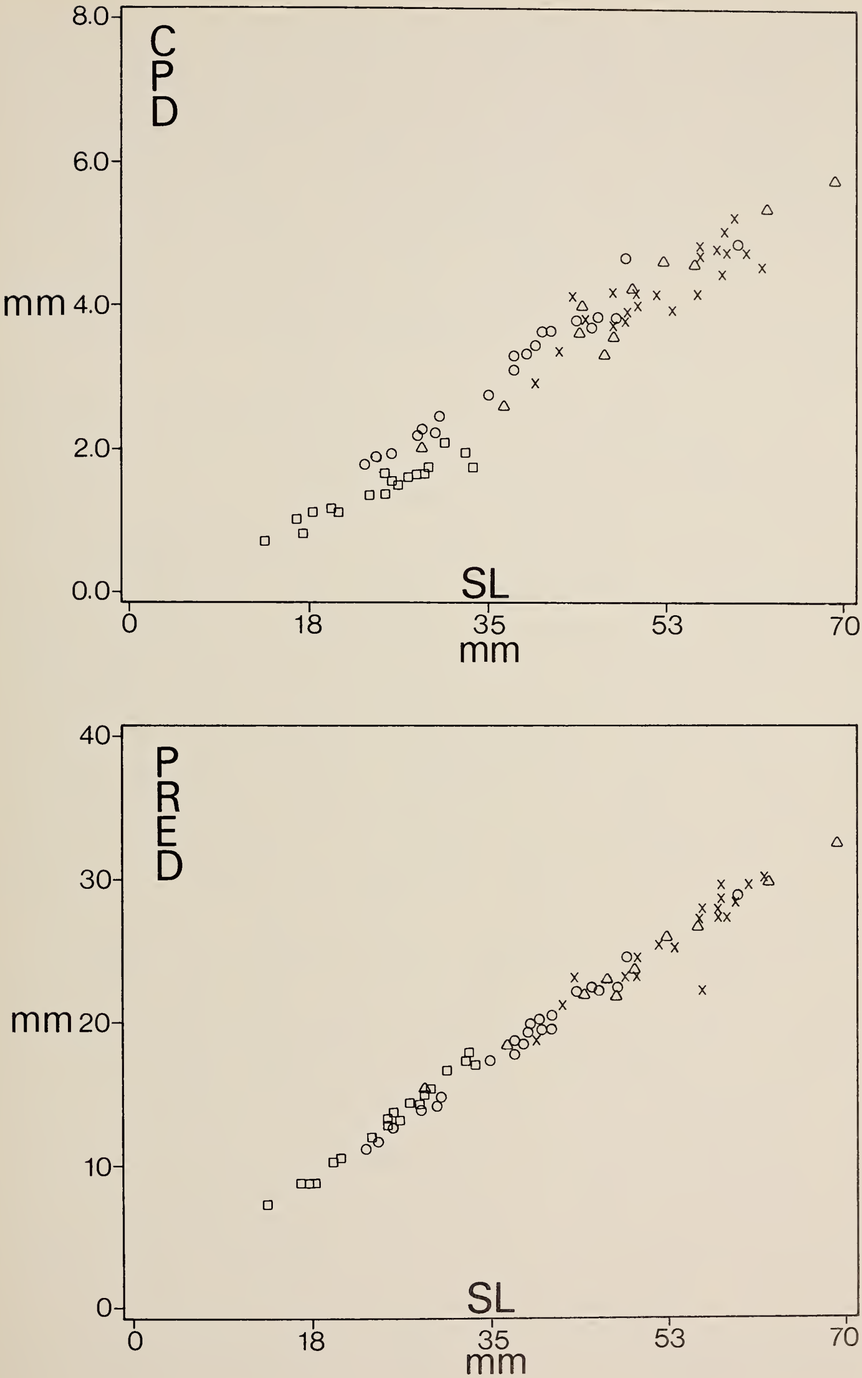


Fig. 3. *Triphoturus*. Upper: caudal peduncle depth (CPD) plotted against standard length (SL). Lower: predorsal length (PRED) plotted against standard length (SL). Symbols as in Figure 1. All measurements in mm.

through outer ventral base) (Figs 5, 7). The PO_3 is raised out of the series and Pol_2 is typically on or behind the vertical through the adipose origin. Atypically (one specimen only), Pol_2 may be situated slightly in advance of the vertical through the adipose origin (Fig. 5A). Variation in individual photophore position also includes the PO_4, PVO_1, SAO_1, SAO_2, and Prc_2 photophores (see Description). Such intraspecific variation is well documented in the closely related genus *Lampanyctus* (Nafpaktitis *et al.* 1977; Hulley 1981) and has no specific taxonomic value. Infracaudal gland structure in specimens of the *T. mexicanus* species-group is similar and the infracaudal gland always extends more than 70 per cent of CPL. It is therefore concluded that photophore pattern and infracaudal gland structure and length would substantiate the identification of only two species.

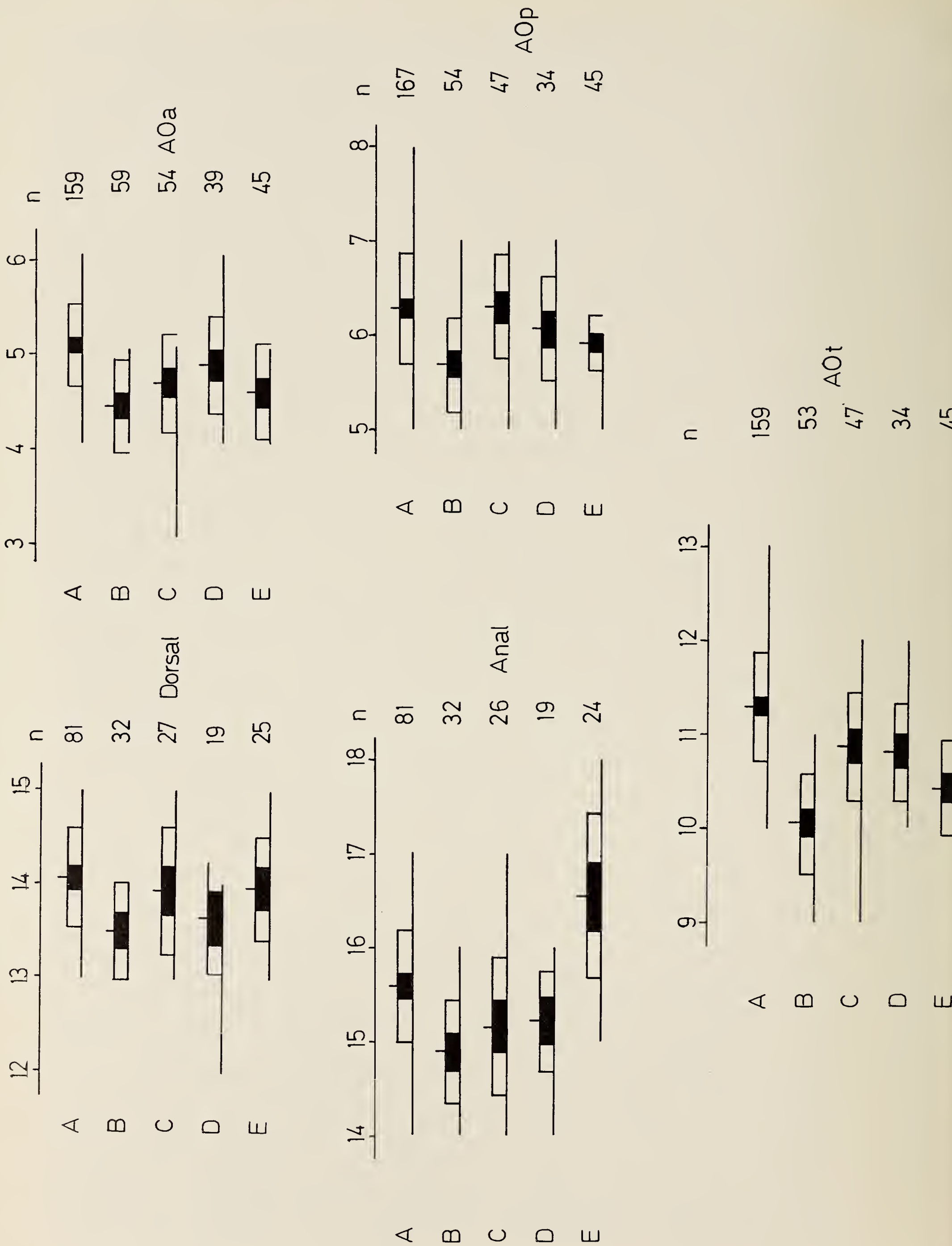
Anal and GRl values (and consequently GRt) would support this conclusion (Fig. 4), as would differences in maximum size. Specimens in the *T. nigrescens* species-group attain a maximum SL of about 40 mm (Nafpaktitis & Nafpaktitis 1969; Wisner 1976; Parin *et al.* 1977; Hulley 1984, in press); the value of 74 mm for *M. micropterum* given by Weber & de Beaufort (1913) is erroneous, since it is based on the length given by Brauer (1906) for ZMB 17614, now known to be *Lampanyctus isaacsi* (Hulley 1981). Specimens in the *T. mexicanus* species-group attain a maximum SL of about 70 mm in both the eastern North and eastern Central–South Pacific (Bolin 1939; Beebe & Van der Pyl 1944; Bussing 1965; Berry & Perkins 1966; Craddock & Mead 1970; Parin *et al.* 1973; Wisner 1976; Childress *et al.* 1980; Neighbours & Nafpaktitis 1982; Imsand 1982). Holton (1969) reported a maximum (?total) length of 100 mm for specimens from off California. The employment of maximum size as a diagnostic should, however, be treated with extreme caution, since it is known that certain myctophids (e.g. *Diaphus brachycephalus*) exhibit dwarfing, i.e. smaller maximum size and smaller size at sexual maturity, in regions of low primary productivity within their distributional range (Hulley 1981).

The *T. mexicanus* species-group is said to comprise two species and a possible subspecies, based on vertebral and gill-raker counts. However, the general tendency is for teleost populations living in warm waters to have less vertebrae than closely related populations living in cool waters, and that these differences are due, in the main, to environmental temperatures prevailing during early development (Fowler 1970; Johnson & Feltes 1984). Modal values and ranges in vertebral counts for specimens from the Gulf of California (32; 30–33) are less than those for specimens from the California Current region (34; 32–36) (Wisner 1976, table 27) and may well be associated with differences in surface water temperatures in the two areas during the spring–summer spawning peak (Ahlstrom 1972; Imsand 1974, 1982; Moser *et al.* 1974). Concomitant with these differences in vertebral count, are differences in serial meristics. Specimens from the Gulf (Group B) have a significantly lower number of dorsal (t −5,12 df 111) and anal (t −5,80 df 111) fin rays, and AOa (t −9,45 df 216) and AOp (t −6,63 df 214) photophores than specimens from the California Current region

(Group A) (Fig. 4). Group B specimens also vary from Group A specimens in possessing higher GRl, and hence GRt counts (t 6,95 df 111; t 6,63 df 111, respectively). The low weighting to the taxonomic significance of GRl variation has already been noted above. Therefore the recognition of a separate subspecies for the Gulf of California specimens does not appear to be warranted. This is supported by the fact that values for D, A, AOa and AOp counts of specimens from the Middle American Trench (Group C), just to the south of the mouth of the Gulf, appear to be somewhat intermediate between those of Groups A and B (Fig. 4). Both GRu and GRl counts in these Group C specimens approximate those for California Current region (Group A) specimens.

Specimens from the eastern Central and South Pacific (Group D: representing *T. oculeus*) may be distinguished meristically from specimens from Middle American Trench (Group C) only by their lower number of gill rakers (GRu: t −14,29 df 46; GRl: t −8,37 df 46; GRt: t −11,56 df 46). Dorsal, anal and AO counts are not significantly different, and mirror equivalent modal values and ranges in vertebral count (Wisner 1976, table 27). The identity of *T. oculeus* is therefore based solely on gill-raker count and on pigmentation of the larvae (Moser & Ahlstrom 1970; Ahlstrom 1971). However, the taxonomic value of these gill-raker differences at the species level is questionable, especially in view of the lack of diagnostic photophore characters. As pointed out above, variations in gill-raker count (both GRu and GRl values) may not be species-specific, especially when they are not corroborated by differences in photophore grouping and/or supra- and infracaudal gland structure. Gill-raker variation is then only interpreted in terms of population differences. This is applicable to both geographically continuous populations (*Diaphus dumerilii*) and to geographically separated populations (*Hygophum hygomii*) (Hulley 1981), as is probably the case in Group D specimens. This is supported by the fact that specimens from off Panama and Costa Rica were found to have GR counts both of 3 + 1 + 10 (9–11) (LACM 33603–18 (3), LACM 33676–7 (4), LACM 33696–11 (4), SU 65711 (2)) and of 4 + 1 + 10–11 (SU 46829 (2)). Furthermore, one of the syntypes of *Myctophum oculeum* (MCZ 35187) has GR 4 + 1 + 10 (left side) and GR 3 + 1 + 10 (right side).

On the other hand, larval characters (including pigmentation) apparently show a considerable degree of variation within a myctophid species: two larval forms of *Hygophum proximum* are found in the northern Indian Ocean (Pertseva-Ostroumova 1974), while only one adult species, exhibiting clinal variation, has been recognized (Nafpaktitis & Nafpaktitis 1969); three larval forms for the *Hygophum macrochir*-complex in the eastern Central Atlantic have been found (Moser & Ahlstrom 1974), but only two adult species are recognized (Nafpaktitis *et al.* 1977; Hulley 1981). Two hypotheses about larval form are therefore possible: either, that one species may have two or more larval forms; or that adults of the second species have not been captured or recognized. In view of the extensive sampling programmes and taxonomic investigations, particularly in the eastern Central Atlantic and the Arabian Sea, the latter hypothesis seems to



Dorsal
n 81 32 27 19 25
A B C D E
12 13 14 15
Anal
n 81 32 26 19 24
A B C D E
14 15 16 17 18
AOa
n 159 59 54 39 45
A B C D E
3 4 5 6
AOp
n 167 54 47 34 45
A B C D E
5 6 7 8
AOt
n 159 53 47 34 45
A B C D E
9 10 11 12 13

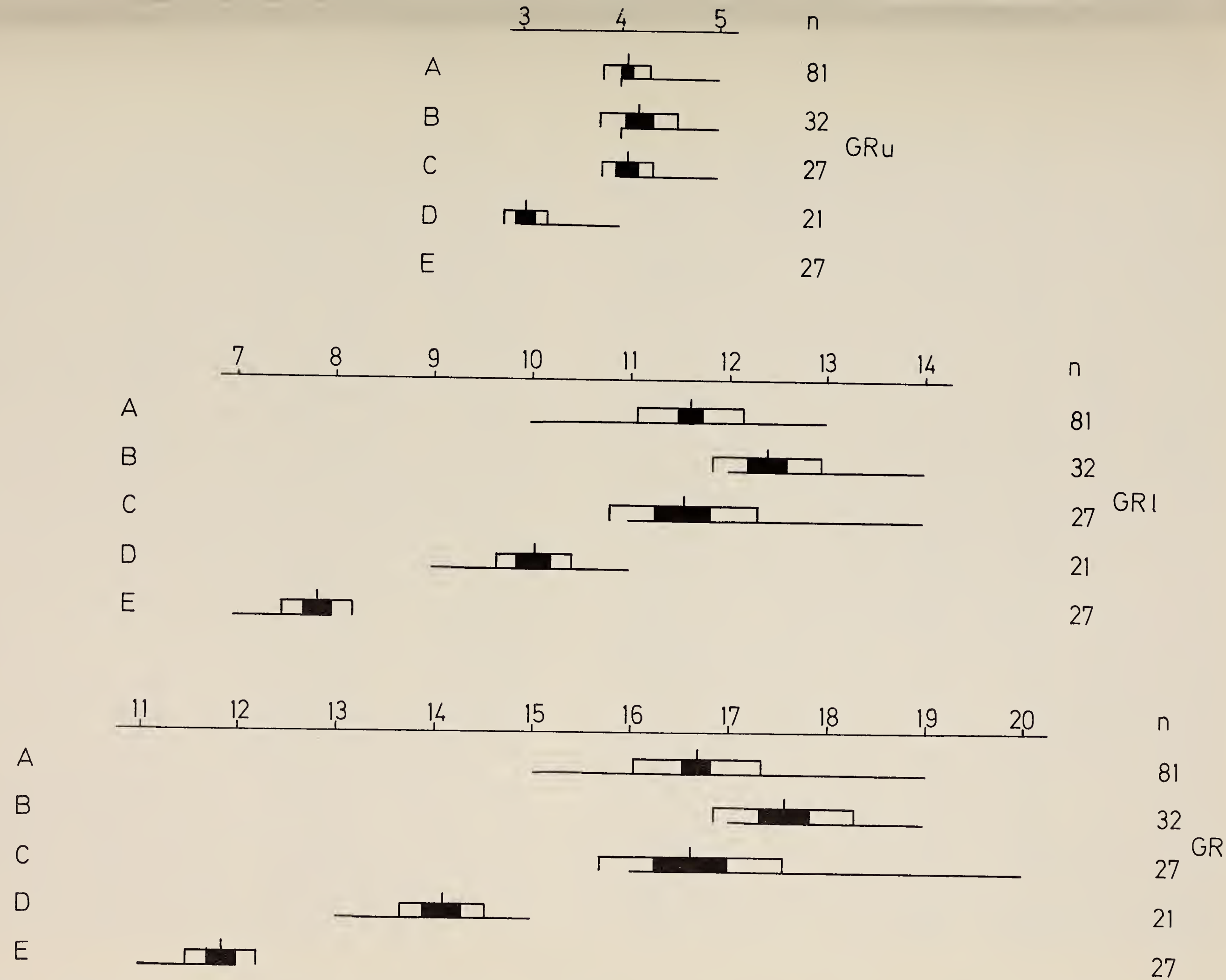


Fig. 4. *Triphoturus*. Meristics plotted according to the method of Hubbs & Hubbs (1953). A—Group A; B—Group B; C—Group C; D—Group D; E—Group E; n = number of counts used to construct the particular graph.

be unlikely for *Hygophum macrochir* and *H. proximum*. Larval diagnostics for *Triphoturus* in the eastern Central Pacific would appear to be unresolved as yet. Ahlstrom (1971: 31) stated that '*at least two species* (my italics) of *Triphoturus* were taken in the EASTROPAC area' (13°N–20°S, 85°W–126°W), a region potentially occupied at least by *T. nigrescens*, *T. mexicanus* and *T. oculeus*, if the latter species is valid (*fide* Parin *et al.* 1973, fig. 18; Wisner 1976, fig. 156; and above data for SU 46829). On the evidence presented by meristics and larval characters, Group D specimens are therefore not considered specifically distinct, and at best can only be recognized as a 'southern' population of *T. mexicanus*.

Morphometric values (Table 2) would not substantiate the differentiation of more than two species. There is little difference in the scatterplots for the various groups (Figs 1–3), although in general, specimens of Group E (corresponding to *T. nigrescens*) appear to be more slender, with the origin of the dorsal fin located somewhat more posteriorly than in Groups A, B, C, and D (corresponding to *T. mexicanus*) (Figs 2–3). Analysis of the data reveals that there is a significant ($F = 6{,}86$ df 1, 87) difference in the case of the slopes of the regressions of CPD vs SL when Group E data are compared to combined data for Groups A, B, C, and D.

In summary then, the genus *Triphoturus* is considered to comprise only two species, *T. nigrescens* and *T. mexicanus*, the latter with a 'northern' and a 'southern' population. Specimens from the Gulf of California represent ecophenotypic variants of the 'northern' population.

SYSTEMATIC ACCOUNT

Genus *Triphoturus* Fraser-Brunner, 1949

Type-species. Myctophum (Lampanyctus) micropterum Brauer, 1906 (= *Myctophum (Lampanyctus) nigrescens* Brauer, 1904) (by original designation).

Mouth large, jaws extending well behind vertical through posterior margin of orbit, with maxillary abruptly enlarged posteriorly. Base of anal fin longer than base of dorsal fin. Pectoral fins small. Dn absent, Vn present. Five PO, with PO_4 elevated and anteriorly displaced to above PO_3. VLO at or a little above lateral line. Five VO, with VO_2 elevated and anteriorly displaced to in front of the vertical through VO_1, and with VO_3 either level, raised or elevated. SAO series markedly angulate. AO series divided into AOa and AOp, both level. Two Pol. Three Prc in an oblique line. Series of overlapping, luminous scales supracaudally and infracaudally in both sexes, immediately in front of procurrent caudal rays.

Two species.

KEY TO SPECIES

1a. VO_3 highly elevated, touching line through VO_2 and SAO_1; PO_3 raised out of series; VLO well behind vertical through outer ventral base; GR 3–5 + 1 + 9–14, total 13–20 .... *T. mexicanus*

1b. VO_3 level or raised, but always well below line joining VO_2 and SAO_1; PO_3 level with PO_2 and PO_5; VLO on or before vertical through outer ventral base; GR 3 + 1 + 7–8, total 11–12 .... *T. nigrescens*

Triphoturus mexicanus (Gilbert, 1890)

Fig. 5

Myctophum mexicanum Gilbert, 1890: 51 (lectotype USNM 76343—Gulf of California; paralectotypes SU 68 (3)—25°59′45″N 111°03′30″W; Böhlke 1953).
Scopelus mexicanus Lütken, 1892: 266.
Nannobrachium mexicanum Goode & Bean, 1895: 512.
Myctophum oculeum Garman, 1899: 260, pl. LVI, fig. 2 (19 syntypes: MCZ 28500, 34945, 34946, 35162, 35182, 35185, 35187, 35189, USNM 120422—eastern Pacific; Paxton 1979).
Myctophum (Lampanyctus) mexicanum Brauer, 1904: 396.
Myctophum (Lampanyctus) oculeum Brauer, 1906: 167.
Lampanyctus mexicanus: Parr, 1928: 84 (key); 1931: 25 (key), 30, fig. 12. Bolin, 1939: 135, fig. 21. Beebe & van der Pyl, 1944: 84, fig. 17.
Lampanyctus oculeus: Parr, 1928: 85 (key).
Lampanyctus (Triphoturus) mexicanus: Fraser-Brunner, 1949: 1084, fig. (key). Berry & Perkins, 1966: 660, fig. 22C.
Triphoturus mexicanus: Bussing, 1965: 203. Bekker, 1967: 179. Paxton, 1967: 424, figs 11, 14, 16. Ahlstrom, 1969: 41; 1971: 31; 1972: x, 64–124. Craddock & Mead, 1970: 3.31. Ebeling *et al.*, 1970: 4, figs 1–4. Robison, 1972: 448, figs 3–4. Paxton, 1972: 6. Brewer, 1973: 23, fig. 10B. McNulty & Nafpaktitis, 1976: 579, pls 1–8. Childress *et al.*, 1980: 28, figs 1, 4. Pieper & Bargo, 1980: 935, figs 1–4. Neighbors & Nafpaktitis, 1982: 208, figs 1, 2. Barnett, 1983: 248. Loeb *et al.*, 1983*a*: 134; 1983*b*: 155, figs 1, 2, 7.
Triphoturus oculeus: Ahlstrom, 1971: 31.

Material

Types. Myctophum mexicanum: lectotype, USNM 76343; paralectotypes, SU 68 (2). *Myctophum oculeum:* syntypes, MCZ 28500 (3), 35185 (1), 35187 (1).

Other. CAS 24312 (30), Santa Catalina Islands; CAS 47824 (5), off Baja California; LACM 31125–27 (27), Middle American Trench (22°21′N 108°12′W–22°25′N 108°29′W); LACM 33603–18 (3), 08°57′30″N 88°05′00″W; LACM 33696–11 (4), 05°28′00″N 82°10′00″W; LACM 33676–7 (4), 05°29′30″N 82°33′00″W; LACM 39201–1 (48), San Pedro Basin (010°T from Long Point Light, 6,0 miles); SAM–24926 (3), 33°40′N–33°45′N, 118°27′W–118°18′W; SAM–30897 (5), 33°19′S 73°39′W; SU 46808 (30), Gulf of Mexico; SU 46829 (2), Panama; SU 65711 (2), Panama.

Description

Meristics and measurements are given in Tables 1–2 and Figure 4.

Origin of dorsal fin well behind vertical through ventral base, usually nearer to tip of snout than to end of lateral line; origin of anal fin under middle of dorsal base or slightly more posterior; origin of adipose fin about on vertical through last anal ray. Pectoral fins small, reaching to about PO_4; ventral fins extending slightly posterior to VO_4.

Dn absent; Vn small, at anteroventral margin of orbit. Op_2 at about level of upper, expanded end of maxillary. Five PO, with PO_1–PO_2 interspace greatest,

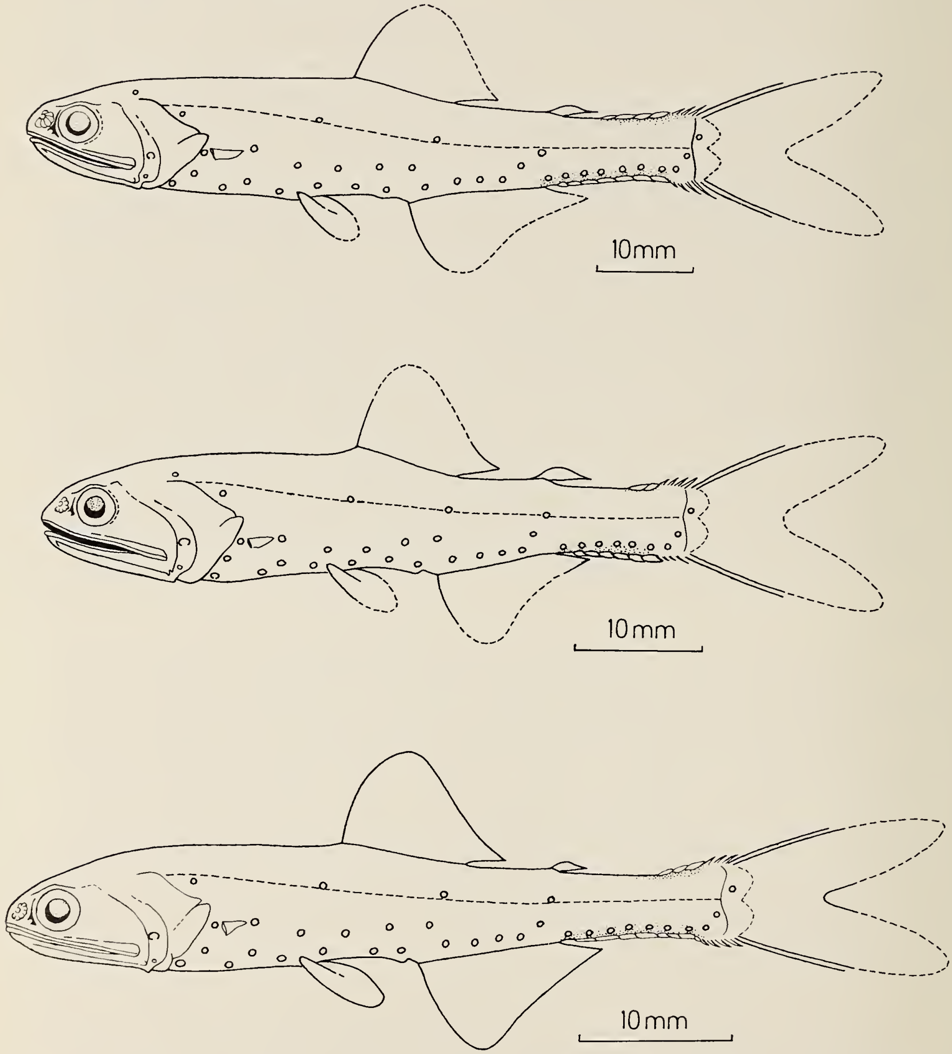


Fig. 5. *Triphoturus mexicanus*. Upper: southern population (MCZ 56962, 33°19'S 73°39'W, SL 68,7 mm). Middle: northern population (SU 46808, Gulf of California, SL 49,5 mm). Lower: northern population (LACM 39201–1, San Pedro Basin, California, SL 47,6 mm).

with PO_3 raised, and with PO_4 elevated and anteriorly displaced to directly on or slightly behind vertical through PO_3 and at level of upper pectoral base or higher. PVO_1 above PO_1–PO_2 interspace, closer to PO_1 than to PO_2 and below level of Op_2; PVO_2 well behind vertical through PVO_1 and below level of upper end of pectoral base. PLO well in advance of vertical through PVO_1, about one photophore diameter below lateral line. VLO behind vertical through ventral base, on vertical through VO_1, and touching dorsal edge of lateral line. Five VO, with VO_2 highly elevated and anteriorly displaced to vertical through outer ventral base; with VO_3 highly elevated, touching line joining VO_2 and SAO_1. SAO series markedly angulate; with SAO_1 midway between VO_4 and VO_5 or closer to VO_5 and slightly above level of VO_2; with SAO_2 above or slightly behind anal origin and at or above level of SAO_1; and with SAO_3 behind vertical through anal origin, touching dorsal edge of lateral line. AOa level, with AOa^1–AOa^2 interspace greatest; AOp level, all behind base of last anal ray. Two Pol, with Pol_1 behind last AOa, and with Pol_2 on or behind vertical through adipose origin, touching dorsal edge of lateral line. Three Prc, in straight ascending line, with Prc_2 nearer to Prc_1 and on or touching line through centres of Prc_1 and Prc_3, and with Prc_3 above level of lateral line.

Supracaudal gland consisting of 3–4 overlapping, luminous scales; infracaudal gland elongate (greater than 70% CPL), with 4–7 overlapping, luminous scales.

Maximum length about 70 mm.

Distribution

Vertical distribution. California Current region: day 200–700 m (maximum 400–500 m), night 50–200 m (maximum 100–200 m). Gulf of California: day 200–700 m (maximum 400–500 m), night 25–550 m (maximum 200–300 m) (Imsand 1982).

The geographic distribution of the species is given in Figure 8.

Triphoturus mexicanus apparently possesses a disjunct distribution in the eastern Pacific Ocean. It is known from throughout the Gulf of California, where it is the dominant midwater fish species between 25°N and 29°N. In the California Current region the species occurs between 38°N and about 20°N, but offshore may extend southwards to 13°N at 127°W. Off the coasts of Central and South America it has been taken from 13°N to about 35°S. Towards its southern limit the species has only been recorded east of 76°W, but off the coast of Peru it may extend westwards to about 95°W.

Triphoturus nigrescens (Brauer, 1904)

Figs 6, 7

Myctophum (Lampanyctus) nigrescens Brauer, 1904: 403 (syntypes: ZMB 17617—03°24′06″S 58°38′01″E; ZMB 22379—02°38′09″S 63°37′09″E); 1906: 241, fig. 158.

Myctophum (Lampanyctus) micropterum Brauer, 1906: 239, fig. 157 (*partim*) (lectotype: ZMB 17616: 02°43′08″S 61°12′06″E; Hulley 1981: 205).

Lampanyctus microchir Gilbert, 1913: 101 (holotype: USNM 74468—Suruga Bay, Japan). Parr, 1928: 85 (key).
?*Myctophum micropterum:* Weber & de Beaufort, 1913: 154, fig. 59.
non Myctophum (Lampanyctus) micropterum: Pappenheim, 1914: 197 (= *Lampanyctus isaacsi* Wisner, 1974).
Lampanyctus nigrescens: Parr, 1928: 84 (key).
Lampanyctus micropterus: Parr, 1928: 85 (key).
Lampanyctus (Triphoturus) microchir Fraser-Brunner, 1949: 1083, fig. (key). Berry & Perkins, 1966: 660, fig. 22C.
Lampanyctus (Triphoturus) micropterus Fraser-Brunner, 1949: 1083, fig. (key).
Lampanyctus (Triphoturus) nigrescens Fraser-Brunner, 1949: 1083, fig. (key). Berry & Perkins, 1966: 660, fig. 22C.
Triphoturus microchir: Bekker, 1967: 179. Nafpaktitis & Nafpaktitis, 1969: 55, figs 62, 70. Legand *et al.*, 1972: 306, fig. 27. Kotthaus, 1972: 29, fig. 284. Clarke, 1973: 406, fig. 12; 1980: 625, figs 1–4. Hartmann & Clarke, 1975: 636. Parin *et al.*, 1973: 114, fig. 19; 1977: 125, fig. 21.
Triphoturus nigrescens: Paxton, 1972: 6. Wisner, 1976: 165, fig. 155. Loeb, 1979*a*: 178; 1979*b*: 789, fig. 10; 1980: 192. Barnett, 1983: 284; 1984: 201. Hulley, 1984: 90, fig. 19. Paxton *et al.*, in press.

Material

Types. Lampanyctus microchir: holotype, USNM 74468. *Myctophum (Lampanyctus) micropterum:* lectotype, ZMB 17616. *Myctophum (Lampanyctus) nigrescens:* syntypes, ZMB 17617, 22379.

Other. See Table 3.

Description

Meristics and measurements are given in Tables 1–2 and Figure 4.

Origin of dorsal fin well behind vertical through ventral base, nearer to end of lateral line than to tip of snout; origin of anal fin under middle of dorsal base or slightly more anterior; origin of adipose fin on vertical through base of last anal ray. Pectoral fins small, reaching to about PO_4; ventral fins extending slightly posterior to VO_4.

Dn absent; Vn small, at anteroventral margin of orbit. Op_2 at about level of upper, expanded end of maxillary. Five PO, with PO_1–PO_2 interspace greatest and with PO_4 elevated and anteriorly displaced to directly on, anterior to, or behind vertical through PO_3 and at level of upper pectoral base or higher. PVO_1 above PO_1–PO_2 interspace, closer to PO_1 than to PO_2 and at about level of Op_2; PVO_2 on or only slightly behind vertical through PVO_1 and below level of upper pectoral base. PLO well in advance of vertical through upper pectoral base, at or less than one photophore diameter below lateral line. VLO slightly anterior to vertical through ventral base, touching dorsal edge of lateral line. Five VO, with VO_2 highly elevated and anteriorly displaced to before vertical through VO_1; VO_3 level or somewhat raised, never touching line joining VO_2 and SAO_1. SAO series markedly angulate, with SAO_1 above VO_3–VO_4 interspace or above VO_4 and at about level of ventral margin of orbit, with SAO_2 above anal origin and at level of SAO_1, and with SAO_3 behind vertical through anal origin, touching dorsal edge of lateral line. AOa level, with AOa^1–AOa^2 interspace greatest; AOp level, all behind base of last anal ray. Two Pol, with Pol_1 behind last AOa

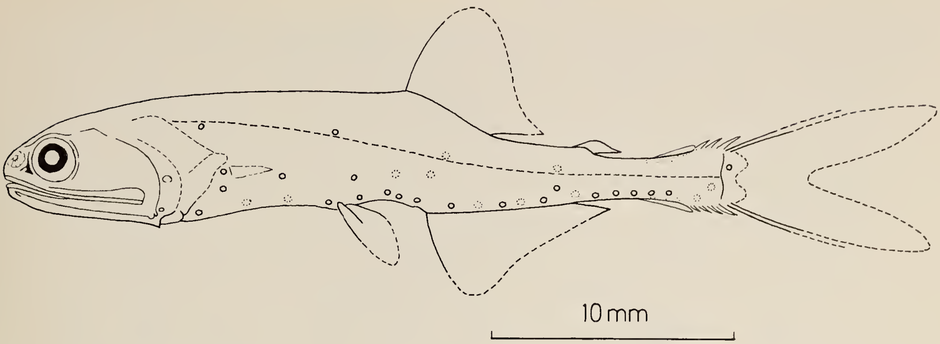


Fig. 6. *Triphoturus nigrescens*. Syntype (ZMB 17617, 'Valdivia' Station 231, 03°24'06"S 58°38'01"E, SL 29,3 mm), now designated as lectotype.

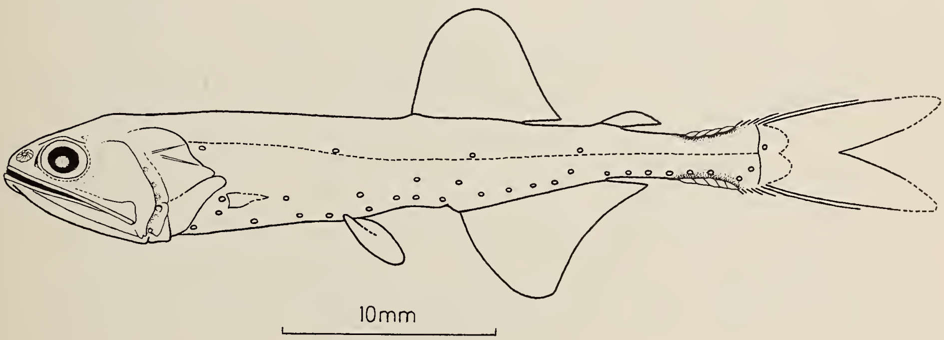


Fig. 7. *Triphoturus nigrescens* (SAM–28094, 30°05,5'S 31°57,0'E, SL 33,6 mm).

and with Pol_2 in advance of vertical through adipose origin, touching dorsal edge of lateral line. Three Prc, in straight ascending line, with Prc_2 nearer Prc_1 and touching line through centres of Prc_1 and Prc_3, and Prc_3 above level of lateral line.

Supracaudal gland consisting of four overlapping, luminous scales; infracaudal gland short (less than 50% CPL), with five overlapping, luminous scales.

Maximum length 40 mm.

Remarks

Due to the poor state of preservation of one (ZMB 22379) of the two syntypes (Table 1), specimen ZMB 17617 is here designated the lectotype of *Myctophum (Lampanyctus) nigrescens* Brauer, 1904. Comparison of this lectotype with the holotype of *Lampanyctus microchir* Gilbert (USNM 74468) and the lectotype of *Myctophum (Lampanyctus) micropterum* Brauer (ZMB 17616) indicates that only a single species is involved. GR counts are similar (3 + 1 + 8,

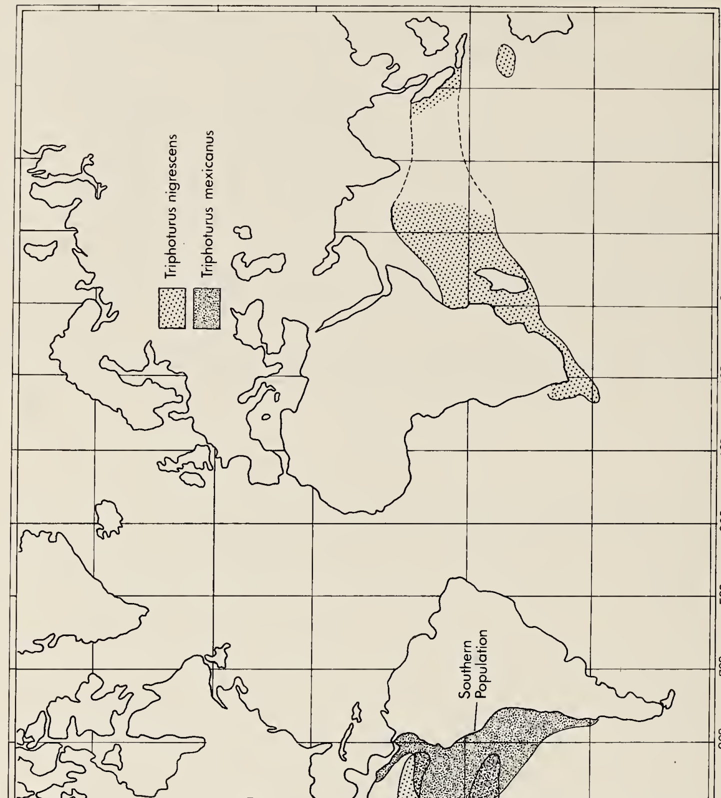


Fig. 8. Distribution of *Triphoturus mexicanus* and *Triphoturus nigrescens*.

total 12), PO_3 is level with PO_2 and PO_5, and VLO is anterior to the vertical through the outer ventral base in all three specimens. Further, in the three specimens the infracaudal gland is shorter than 40 per cent of CPL. Some minor differences in individual photophore position were observed: VO_3 is level with the rest of the series in *L. microchir* and *M. nigrescens*, but slightly raised in *M. micropterum*; SAO_1 is directly above VO_4 in *M. micropterum*, but slightly in advance of the vertical through that photophore in *L. microchir* and *M. nigrescens*; and Prc_2 is on the line joining Prc_1 and Prc_3 in *M. nigrescens*, touches the line in *L. microchir*, and is slightly below the line in *L. micropterus*. Such variation is mirrored in the South African population. Due to damage, D and A counts were not possible for *L. microchir* but the values given by Gilbert (1913) (14 and 17 respectively) fall within the range for *Triphoturus nigrescens* (Fig. 4).

Distribution

Vertical distribution. Off Hawaii: adults day 400–900 m (maximum 650–700 m and 900–1 000 m); adults night 200–300 m and 600–1 000 m; juveniles (less than 20 mm SL) showing little diel migration above 400 m (Imsand 1982).

The geographic distribution of the species is given in Figure 8.

Triphoturus nigrescens is an oceanic, mesopelagic, warm-water species. In the Pacific Ocean it is distributed between about 35°N and 38°S, and extends eastwards in a tongue (0°–08°N) to the coasts of Ecuador, Colombia and Panama. It is absent from upwelled waters of the California and Peru currents. In the western North Pacific it reaches at least to 35°N in the Kuroshio Current. The species is known from South-east Asian Seas and from between 22°S and 38°30′S off the east coast of Australia and in the Tasman Sea (Paxton *et al.* in press). It is distributed in the Indian Ocean between 08°N and 15°S and off the west Australian coast (22°S), and has been reported as far south as 34° in the Agulhas Current. Recent data from the Sea Fisheries Research Institute's phyllosoma sampling cruises off the west coast of South Africa has revealed the presence of the species in the pockets of warm Agulhas Water, that round the Cape of Good Hope and occur in the eastern South Atlantic. These specimens represent the first records of the genus and the species in the Atlantic Ocean and are representative of a Broadly Tropical Pattern (Agulhas Subpattern) of distribution (Hulley 1981).

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REFERENCES

Ahlstrom, E. H. 1969. Mesopelagic and bathypelagic fishes in the California Current region. *Reports of the California Co-operative Oceanic Fisheries Investigations* **13**: 39–44.

Ahlstrom, E. H. 1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* **69** (1): 2–77.

Ahlstrom, E. H. 1972. Distributional atlas of fish larvae in the California Current region: six common mesopelagic fishes—*Vinciguerria lucetia, Triphoturus mexicanus, Stenobrachius leucopsarus, Leuroglossus stilbius, Bathylagus wesethi* and *Bathylagus ochotensis*, 1955 through 1960. *Atlas of the California Co-operative Oceanic Fisheries Investigations* **17**: i–xv, 1–306.

Barlow, G. W. 1961. Causes and significance of morphological variation in fishes. *Systematic Zoology* **10**: 105–117.

Barnett, M. A. 1983. Species structure and temporal stability of mesopelagic fish assemblages in the central gyres of the North and South Pacific Ocean. *Marine Biology* **74** (3): 245–256.

Barnett, M. A. 1984. Mesopelagic fish zoogeography in the central tropical and subtropical Pacific Ocean: species composition and structure at representative locations in three ecosystems. *Marine Biology* **82** (2): 199–208.

Beebe, W. & van der Pyl, M. 1944. Eastern Pacific expeditions of the New York Zoological Society. XXXIII. Pacific Myctophidae. Fishes. *Zoologica, New York* **29** (2): 59–95.

Bekker, V. E. 1967. Luminous anchovies (fam. Myctophidae). *Tichii Okean* **7**. Biologi Tichigi Okeana. 3. Moskow: USSR Academy of Sciences. (In Russian.)

Berry, F. H. & Perkins, H. C. 1966. Survey of pelagic fishes of the California Current area. *Fishery Bulletin of the U.S. Fish and Wildlife Service* **65** (3): 625–682.

Böhlke, J. 1953. A catalogue of the type specimens of recent fishes in the Natural History Museum of Stanford University. *Stanford Ichthyological Bulletin* **5**: 1–168.

Bolin, R. L. 1939. A review of the myctophid fishes of the Pacific coast of the United States and of Lower California. *Stanford Ichthyological Bulletin* **1** (4): 89–156.

Bonaparte, C. L. P. 1840. *Iconografia della fauna Italica per le quattro classi degli animali vertebrati*. 3. Pesci. Roma: Salviucci.

Brauer, A. 1904. Die Gattung *Myctophum. Zoologischer Anzeiger* **28** (10): 377–404.

Brauer, A. 1906. Die Tiefsee-Fische. I. Systematischer Teil. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer 'Valdivia' 1898–1899* **15**: 1–420.

Brewer, G. D. 1973. Midwater fishes from the Gulf of California and the adjacent eastern tropical Pacific. *Contributions in Science. Los Angeles County Museum of Natural History* **242**: 1–47.

Bussing, W. A. 1965. Studies of the midwater fishes of the Peru-Chile Trench. Biology of the Antarctic Seas II. *Antarctic Research Series* **5**: 185–227.

Childress, J. J., Taylor, S. M., Cailliet, G. M. & Price, M. H. 1980. Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off southern California. *Marine Biology* **61** (1): 27–40.

Clarke, T. A. 1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* **71** (2): 401–433.

Clarke, T. A. 1980. Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* **78** (3): 619–640.

Craddock, J. E. & Mead, G. W. 1970. Midwater fishes from the eastern South Pacific Ocean. Scientific results of the Southeast Pacific Expedition. *Scientific Results of the Southeast Pacific Expedition. Anton Bruun Report* **3**: 3.3–3.46.

Ebeling, A. W., Ibara, R. M., Lavenberg, R. J. & Rohlf, F. J. 1970. Ecological groups of deep-sea animals off southern California. *Bulletin of the Los Angeles County Museum of Natural History (Science)* **6**: 1–43.

Fowler, H. W. 1934. Descriptions of new fishes obtained in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Proceedings of the Academy of Natural Sciences of Philadelphia* **85**: 233–367.

Fowler, J. A. 1970. Control of vertebral number in teleosts—an embryological problem. *Quarterly Reviews of Biology* **45**: 148–167.

Fraser-Brunner, A. 1949. A classification of the fishes of the family Myctophidae. *Proceedings of the Zoological Society of London* **118** (4): 1019–1106.

Garman, S. 1899. Reports on an expedition off the west coasts of Mexico, Central and South America, and off the Galapagos Islands in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer 'Albatross' during 1891, Lieut. Commander Z. L. Tanner, U.S.N. commanding. XXVI. The fishes. *Memoirs of the Museum of Comparative Zoology at Harvard College* **24**: 1–431.

Gilbert, C. H. 1890. A preliminary report on the fishes collected by the steamer 'Albatross' on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. *Proceedings of the U.S. National Museum* **13** (797): 49–126.

Gilbert, C. H. 1913. The lantern-fishes of Japan. *Memoirs of the Carnegie Museum* **6** (2): 67–107.

Goode, G. B. & Bean, T. H. 1895. Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers 'Blake', 'Albatross', and 'Fish Hawk' in the northwestern Atlantic, with an atlas containing 417 figures. *Memoirs of the Museum of Comparative Zoology at Harvard College* **1**: 1–553.

Hartmann, A. R. & Clarke, T. A. 1975. The distribution of myctophid fishes across the central equatorial Pacific. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* **73** (3): 633–641.

Holton, A. A. 1969. Feeding behaviour of a vertically migrating lanternfish. *Pacific Science* **23** (3): 325–331.

Hubbs, C. L. & Hubbs, C. 1953. An improved graphical analysis and comparison of series of samples. *Systematic Zoology* **2** (2): 49–57.

Hulley, P. A. 1981. Results of the research cruises of FRV 'Walther Herwig' to South America. LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). *Archiv für Fischereiwissenschaft* **31** (1): 1–300.

Hulley, P. A. 1984. The South African Museum's *Meiring Naude* cruises. Part 14. Family Myctophidae (Osteichthyes, Myctophiformes). *Annals of the South African Museum* **93** (2): 53–96.

Hulley, P. A. In press. Family Myctophidae. *In:* Smith, M. M. & Heemstra, P. C. *eds. Smith's sea fishes.*

Humphries, J. M., Bookstein, F. L., Chernoff, B., Smith, G. R., Elder, R. L. & Poss, S. G. 1981. Multivariate discrimination by shape in relation to size. *Systematic Zoology* **30** (3): 291–308.

Imsand, S. 1974. Population dynamics of two lanternfish: *Triphoturus mexicanus* of the California Current and *T. nigrescens* of the North Pacific Central Gyre. *Biennial Report for the two years ending 30 June 1974, Institute of Marine Sciences, University of California*: 37–38.

Imsand, S. 1982. Abundance in space and time of lanternfishes of the genus *Triphoturus* (Myctophidae) in the Pacific Ocean. Ph.D. thesis: University of California (San Diego).

Johnson, R. K. & Barnett, M. A. 1975. An inverse correlation between meristic characters and food supply in midwater fishes; evidence and possible explanations. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* **73** (2): 284–298.

Johnson, R. K. & Feltes, R. M. 1984. A new species of *Vinciguerria* (Salmoniformes: Photichthyidae) from the Red Sea and the Gulf of Aqaba, with comments on the depauperacy of the Red Sea mesopelagic fish fauna. *Fieldiana: Zoology* (N.S.) **22**: 1–35.

Kotthaus, A. 1972. Fische des Indischen Ozeans. Ergebnisse der ichthyologischen Untersuchungen während der Expedition des Forschungsschiffes 'Meteor' in den Indischen Ozean, Oktober 1964 bis Mai 1965. A. Systematischer Teil, IX. Iniomi (Nachtrag: Fam. Myctophidae). *Meteor Forschungsergebnisse* (D) **12**: 12–35.

Legand, M., Bourret, P., Fourmanoir, P., Perrin, R., Gueredrat, J. A., Michel, A., Repelin, R. & Roger, C. 1972. Relations trophiques et distributions verticales en milieu pélagique dans l'Océan Pacifique intertropical. *Cahiers de l'Office Recherche scientifique et technique Outre-Mer (Série Océanographie)* **10** (4): 304–393.

Loeb, V. J. 1979*a*. Larval fishes in the zooplankton community of the North Pacific Central Gyre. *Marine Biology* **53** (2): 173–191.

Loeb, V. J. 1979*b*. Vertical distribution and development of larval fishes in the North Pacific Central Gyre during summer. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* **77** (4): 777–793.

Loeb, V. J. 1980. Pattern of spatial and species abundance within the larval fish assemblage of the North Pacific Central Gyre during late summer. *Marine Biology* **60** (2/3): 189–200.

Loeb, V. J., Smith, P. E. & Moser, H. G. 1983*a*. Geographical and seasonal patterns of larval fish species structure in the California Current area, 1975. *Reports of the California Co-operative Oceanic Fisheries Investigations* **24**: 132–151.

Loeb, V. J., Smith, P. E. & Moser, H. G. 1983*b*. Recurrent groups of larval fish species in the California Current area. *Reports of the California Co-operative Oceanic Fisheries Investigations* **24**: 152–164.

Lütken, C. F. 1892. Spolia Atlantica. Scopelini Musei Zoologici Universitatis Hauiensis. *Kongelige Danske Videnskabernes Selskabs Skrifter* (6) **7**: 221–297.

McNulty, J. A. & Nafpaktitis, B. G. 1976. The structure and development of the pineal complex in the lanternfish *Triphoturus mexicanus* (family Myctophidae). *Journal of Morphology* **150** (2): 579–605.

Moser, H. G. & Ahlstrom, E. H. 1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. *Bulletin of the Los Angeles County Museum of Natural History (Science)* **7**: 1–145.

Moser, H. G. & Ahlstrom, E. H. 1974. Role of larval stages in systematic investigations of marine teleosts: the Myctophidae, a case study. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* **72** (2): 391–413.

Moser, H. G., Ahlstrom, E. H., Kramer, D. & Stevens, E. G. 1974. Distribution and abundance of fish eggs and larvae in the Gulf of California. *Reports of the California Co-operative Oceanic Fisheries Investigations* **17**: 112–128.

Nafpaktitis, B. G. 1973. A review of the lanternfishes (family Myctophidae) described by Å. Vedel Tåning. *Dana Report* **83**: 1–46.

Nafpaktitis, B. G., Backus, R. H., Craddock, J. E., Haedrich, R. L., Robison, B. H. & Karnella, C. 1977. Fishes of the western North Atlantic. Family Myctophidae. *Memoirs of the Sears Foundation for Marine Research* **1** (7): 13–265.

Nafpaktitis, B. G. & Nafpaktitis, M. 1969. Lanternfishes (family Myctophidae) collected during cruises 3 and 6 of the R/V *Anton Bruun* in the Indian Ocean. *Bulletin of the Los Angeles County Museum of Natural History (Science)* **5**: 1–79.

Neighbors, M. A. & Nafpaktitis, B. G. 1982. Lipid compositions, water contents, swimbladder morphologies and buoyancies of nineteen species of midwater fishes (18 myctophids and 1 neoscopelid). *Marine Biology* **66** (3): 207–215.

Pappenheim, P. 1914. Die Fische der deutschen Südpolar-Expedition 1901–1903. II. Die Tiefseefische. *Deutsche Südpolar-Expedition, 1901–1903* **15** (Zoologie 7): 163–200.

Parin, N. V., Bekker, V. E., Borodulina, O. D. & Tchuvasov, V. M. 1973. Deep-sea pelagic fishes of the south-eastern Pacific Ocean. *Trudy̆ Instituta okeanologii. Akademiya nauk SSSR* **94**: 71–172. (In Russian.)

Parin, N. V., Bekker, V. E., Borodulina, O. D., Karmovskaya, E. S., Fedoryako, B. I., Shcherbachev, J. N., Pokhilskaya, G. N. & Tchuvasov, V. M. 1977. Midwater fishes in the western tropical Pacific Ocean and the seas of the Indo-Australian Archipelago. *Trudy̆ Instituta okeanologii. Akademiya nauk SSSR* **107**: 68–199. (In Russian.)

Parr, A. E. 1928. Deepsea fishes of the order Iniomi from the waters around the Bahama and Bermuda islands, with annotated keys to the Sudidae, Myctophidae, Scopelarchidae, Evermannellidae, Omosudidae, Cetomimidae and Rondeletiidae of the world. *Bulletin of the Bingham Oceanographic Collection* **3** (3): 1–193.

Parr, A. E. 1931. Deepsea fishes from off the western coast of North and Central America. *Bulletin of the Bingham Oceanographic Collection* **2** (4): 1–53.

Paxton, J. R. 1967. A distributional analysis for the lanternfishes (family Myctophidae) of the San Pedro Basin, California. *Copeia* **1967** (2): 422–440.

Paxton, J. R. 1972. Osteology and relationships of the lanternfishes (family Myctophidae). *Science Bulletin. Natural History Museum, Los Angeles County* **13**: 1–81.

Paxton, J. R. 1979. Nominal genera and species of lanternfishes (family Myctophidae). *Contributions in Science. Los Angeles County Museum* **322**: 1–28.

Pertseva-Ostroumova, T. A. 1974. New data on lantern-fish larvae (Myctophidae, Pisces) with oval eyes from the Indian and Pacific oceans. *Trudӯ Instituta okeanologii. Akademiya nauk SSSR* **96**: 77–142. (In Russian.)

Pieper, R. E. & Bargo, B. G. 1980. Acoustic measurements of a migrating layer of the Mexican lampfish, *Triphoturus mexicanus*, at 102 kiloherz. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* **77** (4): 935–942.

Robison, B. H. 1972. Distribution of midwater fishes of the Gulf of California. *Copeia* **1972** (3): 448–461.

Snedecor, G. W. & Cochran, W. 1967. *Statistical methods*. 6th ed. Ames: Iowa State University Press.

Sokal, R. R. & Rohlf, F. J. 1969. *Biometry. The principles and practice of statistics in biological research*. San Francisco: Freeman & Co.

Weber, M. & de Beaufort, L. F. 1913. *The fishes of the Indo-Australian Archipelago*. II. Malacopterygii, Myctophoidea, Ostariophysi: I. Siluroidea. Leiden: Brill.

Wisner, R. L. 1974. Descriptions of five new species of myctophid fishes from the Pacific, Indian and Atlantic oceans. *Occasional Papers of the California Academy of Sciences* **110**: 1–37.

Wisner, R. L. 1976. *The taxonomy and distribution of lanternfishes (family Myctophidae) of the eastern Pacific Ocean*. Washington: U.S. Government Printing Office.

Zar, J. H. 1974. *Biostatistical analysis*. Englewood Cliffs: Prentice-Hall.